Annals of Botany Page 1 of 10
doi:10.1093/aob/mcn127, available online at www.aob.oxfordjournals.org

OXFORD JOURNALS
OXFORD UNIVERSITY PRESS

REVIEW

Indirect Suppression of Photosynthesis on Individual Leaves by Arthropod Herbivory

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Received: 30 April 2008 Returned for revision: 4 June 2008 Accepted: 12 June 2008

• *Background* Herbivory reduces leaf area, disrupts the function of leaves, and ultimately alters yield and productivity. Herbivore damage to foliage typically is assessed in the field by measuring the amount of leaf tissue removed and disrupted. This approach assumes the remaining tissues are unaltered, and plant photosynthesis and water balance function normally. However, recent application of thermal and fluorescent imaging technologies revealed that alterations to photosynthesis and transpiration propagate into remaining undamaged leaf tissue.
• *Scope and Conclusions* This review briefly examines the indirect effects of herbivory on photosynthesis, measured by gas exchange or chlorophyll fluorescence, and identifies four mechanisms contributing to the indirect suppression of photosynthesis in remaining leaf tissues: severed vasculature, altered sink demand, defence-induced autotoxicity, and defence-induced down-regulation of photosynthesis. We review the chlorophyll fluorescence and thermal imaging techniques used to gather layers of spatial data and discuss methods for compiling these layers to achieve greater insight into mechanisms contributing to the indirect suppression of photosynthesis. We also elaborate on a few herbivore-induced gene-regulating mechanisms which modulate photosynthesis and discuss the difficult nature of measuring spatial heterogeneity when combining fluorescence imaging and gas exchange technology. Although few studies have characterized herbivore-induced indirect effects on photosynthesis at the leaf level, an emerging literature suggests that the loss of photosynthetic capacity following herbivory may be greater than direct loss of photosynthetic tissues. Depending on the damage guild, ignoring the indirect suppression of photosynthesis by arthropods and other organisms may lead to an underestimate of their physiological and ecological impacts.

Key words: Chlorophyll fluorescence imaging, thermography, plant–insect interactions, spatial patterns, autotoxicity, induced defences, jasmonates.

INTRODUCTION

Insects consume vast quantities of plant biomass each year, but simply considering the amount of tissue removed may underestimate their impact on yield and ecosystem production. On average, herbivores remove approx. 15 % of primary production in terrestrial ecosystems, but complete removal is not uncommon in out-break years (Cyre and Pace, 1993). Similarly, insects consume approx. 14 % of total global agricultural output (Oerke and Dehne, 1997). This value is relatively low because of the widespread application of pesticides. In the absence of pesticides, losses would exceed 50 % for all major crops (Oerke and Dehne, 1997). Herbivore damage is assessed in agricultural fields by surveying the amount of tissue removed from foliage. This approach, however, assumes that the remaining leaf tissue functions normally. Many types of insect damage affect photosynthesis in undamaged tissues, and these 'indirect' effects on photosynthesis may be considerably greater than the direct removal of leaf area (Welter, 1989; Zangerl *et al.*, 2002).

Insect herbivory, whether defoliation or by feeding on specific tissues (e.g. phloem or xylem), triggers a complex and interacting array of molecular and physiological responses in plants. These responses potentially reduce the photosynthetic capacity in remaining leaf tissues to a greater extent than the direct removal of photosynthetic surface area. For example, the removal of only 5 % of the area of an individual wild parsnip leaf by caterpillars reduced photosynthesis by 20 % in the remaining foliage (Zangerl *et al.*, 2002), and the decline in photosynthesis in the remaining leaf tissue of an oak sapling was equal to the decrease in photosynthesis associated with the actual removal of leaf tissue (Aldea *et al.*, 2006*b*). The mechanisms reducing photosynthesis in remaining leaf tissues are multifaceted, ranging from disruptions in fluid or nutrient transport to self-inflicted reductions in metabolic processes. However, the magnitude of these effects on photosynthesis and the underlying mechanisms are highly variable, depending in large part on the type of feeding damage and the mode of defence deployed by the plant under attack.

In this review, we build upon previous evaluations of the effects of insect herbivory on photosynthesis (Welter, 1989; Peterson and Higley, 2001) by examining feeding-induced spatial heterogeneity in photosynthesis across individual leaves. The application of fluorescence imaging techniques (Rolfe and Scholes, 1995; Baker *et al.*, 2001) is providing new insight into how different damage guilds, including pathogens and insects, affect the component processes of photosynthesis. When combined with other imaging methods such as thermography, the use of reporter genes to follow transcription, and fluorescent dyes that track signalling compounds (e.g. Ca^{2+} ions, H_2O_2), the mechanisms responsible for altering photosynthesis in remaining tissues are being elucidated. The use of geographic image analysis as a tool for making quantitative comparisons of images representing different biological processes is discussed, as

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this method provides the capability to compile many layers of covariate information to reveal new mechanistic insights.

INDIRECT VERSUS DIRECT EFFECTS OF HERBIVORY ON PHOTOSYNTHESIS

Plant responses to arthropod herbivory traditionally have been assessed from the guild perspective, where different insect guilds are defined by their feeding mechanisms (Welter, 1989; Peterson and Higley, 2001). These guilds (e.g. chewing damage, piercing damage, etc.) were established in an effort to recognize 'homogeneity in physiological response' between different attacking agents (arthropods) that alter plant physiological processes in a similar manner (Higley *et al.*, 1993). Using this guild approach, Welter (1989) examined an extensive body of literature across multiple guilds and found over 50 % of all plant–insect interactions resulted in a loss of photosynthetic capacity. Defoliation generally increases photosynthesis, whereas specialized cell-content feeding decreases photosynthesis. Since then, several studies have examined plant responses to different insect feeding guilds and even to different insects within guilds in an effort to develop models for predicting plant response to different feeding mechanisms (see Peterson and Higley, 2001).

A review of the recent literature is not entirely consistent with the conclusions stated by Welter (1989). Feeding on specialized tissues typically reduces photosynthesis, regardless of whether the attacked component is the phloem or xylem (Haile *et al.*, 1999; Macedo *et al.*, 2003*a*, *b*; Heng-Moss *et al.*, 2006), the stem (Macedo *et al.*, 2005, 2007) or general leaf fluids (Haile and Higley, 2003). There is some evidence indicating that increased photosynthesis occurs in the presence of phloem feeding, particularly when the annual photosynthesis rate is estimated (Dungan *et al.*, 2007). In contrast, defoliation injury often does not alter photosynthetic capacity, within plant families (e.g. legumes) or between hardwoods and crops (Peterson *et al.*, 1992, 1996, 2004); however, there are examples where defoliation reduced (Delaney and Higley, 2006) or increased photosynthesis (Turnbull *et al.*, 2007).

The removal of leaf tissue by herbivores represents a 'direct' reduction of photosynthetic capacity. The suppression of photosynthesis in remaining leaf tissue is defined by any one of a number of processes, including damage to the vasculature supplying that tissue, as an 'indirect' effect of herbivory. Arthropods damage xylem or phloem (Welter, 1989), which may alter water transport, stomatal aperture, and sucrose transport and loading, thereby reducing photosynthesis in remaining leaf tissue. Severing tissue vasculature alters leaf hydraulics, and, subsequently, nutrient or osmotica transport (Sack and Holbrook, 2006). If insect feeding is subtle enough to avoid outright cell rupture, modulation of nutrients sequestered by feeding will alter plant osmotica or sink/source relationships (Girousse *et al.*, 2005; Dorchin *et al.*, 2006). These effects also may be mediated by the plant's response. Insect attack, or even the perception of attack, can induce a myriad of defence-related responses while concomitantly reducing the expression of photosynthesis-related genes (Kessler and Baldwin, 2002). In instances where plant defences are constitutively expressed, the release of biocidal compounds against attackers may damage photosynthetic or homeostatic mechanisms vital for plant function (e.g. Zangerl *et al.*, 2002). Indirect effects of herbivory were assigned to four classes: severed vasculature, altered sink demand, defence-related autotoxicity, and defence-induced down-regulation of photosynthesis (Fig. 1).

SEVERED VASCULATURE ALTERS PHOTOSYNTHESIS AND WATER BALANCE

Damage to leaf venation alters leaf hydraulic conductance thereby reducing stomatal conductance and photosynthesis. In the absence of alternative pathways for water transport, the consequences of damage to venation can persist for weeks after the initial injury and lead to leaf desiccation (Sack and Holbrook, 2006). Defoliation injury which severs venation indiscriminately or feeding on specific tissues, may physically obstruct fluid flow with insect mouthparts (stylets) or cell fragments and alter photosynthesis and water balance in remaining leaf tissue (Reddall *et al.*, 2004; Delaney and Higley, 2006). In *Glycine max* (soybean) a form of defoliation (skeletonization) which removes patches of tissue reduced photosynthesis in remaining tissue on damaged leaves and on adjacent undamaged leaflets (Peterson *et al.*, 1998). Interestingly, soybean increased carbon uptake rates and transpiration in remaining leaf tissue when one or two leaflets were completely lost (Suwignyo *et al.*, 1995), but when leaf area removal (no patches) occurred to only part of a leaflet, CO_2 uptake did not decrease in the remaining leaflet tissue (Peterson *et al.*, 2004).

Aldea *et al.* (2005) confirmed that skeletonizing of soybean leaves by Japanese beetles substantially increased water loss from the cut edges. Damaging the interveinal tissue increased transpiration by 150 % for up to 4 d post-injury. While this uncontrolled water loss had no detectable effect on CO_2 exchange, severed vasculature induced a short-lived (2 d) increase in photosynthetic efficiency (Φ_{PSII}) in undamaged tissue of damaged leaves. The increase in Φ_{PSII} without a corresponding increase in CO_2 uptake suggests that insect damage transiently decoupled photosynthetic electron transport from carbon assimilation (Aldea *et al.*, 2005). Severing veins and interveinal tissue alters the hydraulic construction of leaves by reducing resistance exponentially with increasing damage (Nardini and Salleo, 2005).

The effects of defoliation on photosynthesis seem to be less predictable than damage caused by other feeding guilds. In hardwoods, leaf gall and fungal damage consistently reduced Φ_{PSII} at distances $\geq$1 cm from the point of direct damage, whereas defoliation resulted in only highly local reductions ($<$1 mm) in Φ_{PSII} (Aldea *et al.*, 2006*b*). With one exception, defoliation of soybean and *Arabidopsis thaliana* leaves caused only a minimal reduction in Φ_{PSII}. When compared with the mild effect of feeding by larger 4th instar *Trichoplusia ni* larvae, damage by smaller 1st instars severely depressed Φ_{PSII}, maximum photosynthetic efficiency, and nonphotochemical quenching (NPQ) in arabidopsis (Tang *et al.*, 2006). The greater perimeter-to-area ratio of the numerous small holes produced by 1st instars

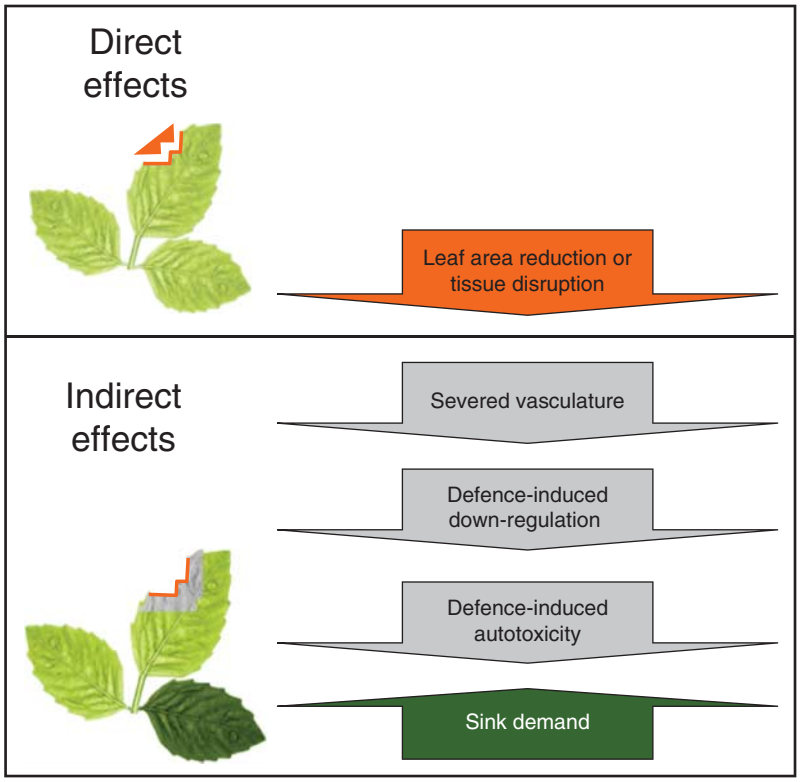

FIG. 1. Conceptual model of the direct effect of herbivory (removal of leaf area) and the indirect effects of herbivore damage to foliage on photosynthesis in the remaining leaf tissues.

compared with 4th instars may have promoted greater rates of water loss from the cut edges and a corresponding reduction in Φ_{PSII}. That the reduction in Φ_{PSII} could be reversed by exposing the leaf to higher concentrations of CO_2, suggests that profligate water loss near cut edges reduced Φ_{PSII} and increased NPQ by causing localized stomatal closure in the remaining undamaged leaf tissue.

HERBIVORY ALTERS SINK DEMAND

In instances where plants respond to herbivory with increased CO_2 uptake, the mechanism typically is linked to compensation or an increase in the sink demand within the leaf. An extensive literature exists on photosynthetic compensation for arthropod herbivory (see Trumble *et al.*, 1993); yet recent examples have highlighted previously uncharacterized compensatory responses. For some gall-forming insects, gall tissue itself increases photosynthesis relative to uninjured tissue. In *Ilex aquifolium* (holly), increased Φ_{PSII} and electron transport rate enhanced photosynthesis (Retuerto *et al.*, 2004) whereas a reduction in respiration in *Acacia pycnantha* galls contributed to an increase in net photosynthesis (Dorchin *et al.*, 2006). While phloem feeding increased whole-canopy photosynthesis in beech trees, perhaps through a reduction in photosynthate build-up, the mechanism remains unclear and may be as simple as herbivore preference for hosts with higher rates of photosynthesis (Dungan *et al.*, 2007).

In other galls of hardwoods, feeding damage reduced photosynthesis and altered water balance. Gall formation in red maple, pignut hickory and black oak reduced Φ_{PSII}, but increased NPQ, indicating a down-regulation of the PSII reaction centres in the area around galls (Aldea *et al.*, 2006*b*). A sharp reduction in leaf temperature near galls suggests that transpiration was greater and fluid and nutrient transport increased near the point of damage (Macfall *et al.*, 1994). In contrast to gall-forming insects, a leaf-mining moth that lives enclosed within leaf tissue of apple trees, reduced carbon assimilation rates by decreasing transpiration (Pincebourd *et al.*, 2006); however, the effects of this guild on plant physiology have yet to be evaluated using fluorescence and thermal imaging.

Defoliation also may increase photosynthesis by altering sink demand, but concerns over what and how remaining tissues were measured have been noted (Welter, 1989). By enclosing severed edges within gas exchange cuvettes or measuring treatment effects on leaves where adjacent leaves were removed (within-plant controls), the data may not accurately describe plant responses specific to the herbivory treatment. Despite these potential limitations, data suggest that defoliation, as well as removal of reproductive and other vegetative sinks, may improve photosynthesis in remaining leaf tissue by increasing carboxylation efficiency and the rate of RuBP regeneration (Layne and Flore, 1992; Holman and Oosterhuis, 1999; Thomson *et al.*, 2003; Ozaki *et al.*, 2004; Turnbull *et al.*, 2007).

PLANT RESPONSES INDUCE AUTOTOXICITY

Plants invest in defences differently depending upon taxa, habitat, and resource availability (Fine *et al.*, 2006), and many chemical defences are known for both model plant systems and across less-studied taxa (Coley and Barone, 1996; Berenbaum and Zangerl, 2008). Plants run the risk of autotoxicity because of the biocidal properties of many secondary compounds. Although *in vivo* studies of autotoxicity are limited, photosynthesis may be severely reduced for some species. For example, wild parsnip (*Pastinaca sativa*) contains an arsenal of defence compounds including furanocoumarins, which are photoactivated and biocidal against a variety of organisms (Arnason *et al.*, 1991). Furanocoumarins are contained in oil tubes under positive pressure and bleed profusely from the wounding site (Gog *et al.*, 2005). When herbivores sever these tubes, the release of furanocoumarins reduces Φ_{PSII} and gas exchange at considerable distances from the actual point of insect damage (Zangerl *et al.*, 2002; Gog *et al.*, 2005).

The autotoxic effect of defensive compounds on photosynthesis is highly species specific. Essential oils derived from parsley (*Petroselinum crispum*), wild parsnip and rough lemon (*Citrus jambhiri*) reduce Φ_{PSII} when applied to leaves of conspecifics; however, oils from parsley affected a 2-fold greater area than the other species (Gog *et al.*, 2005). Baldwin and Callahan (1993) fed nicotine to two species of tobacco (*Nicotiana sylvestris*, *N. glauca*) that naturally synthesized this alkaloid as a defence (Kessler and Baldwin, 2002), and to two other solanaceous species lacking nicotine (*Datura stramonium*, *Solanum lycopersicum*). Photosynthetic rates declined in both species that synthesize nicotine but only in one that did not (*S. lycopersicum*). Priming plants with nicotine (simulated damage) prior to being fed reduced photosynthetic rates more than in damaged-unfed plants, linking nicotine toxicity to the reduction in photosynthesis. Reduced photosynthesis, in part, reduced total growth and fitness. Subsequently, plants producing nicotine constitutively or upon the induction of defence are likely to endure autotoxicity and reductions in fitness.

DEFENCE-INDUCED DOWN-REGULATION OF PHOTOSYNTHESIS-RELATED GENES

Jasmonates play a central role in regulating plant defence responses to herbivores. The mechanism by which herbivore-induced jasmonate synthesis promotes global reprogramming of defence gene expression and the regulation of this response have been reviewed recently (Howe and Jander, 2008). While jasmonates induce defences, they also inhibit growth and photosynthesis (Giri *et al.*, 2006; Zavala and Baldwin, 2006; Yan *et al.*, 2007).

Transcriptional analysis of plant–herbivore interactions revealed that photosynthesis-related genes are down-regulated after attack (e.g. Hui *et al.*, 2003; Reymond *et al.*, 2004); however, few studies have demonstrated the effects of herbivore attack on photosynthesis at the proteome and physiological levels. Attack by herbivores or pathogens reduces transcription of the primary enzyme responsible for carbon fixation, ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCase; Hermsmeier *et al.*, 2001; Hahlbrock *et al.*, 2003; Hui *et al.*, 2003). Using two-dimensional electrophoresis, Giri *et al.* (2006) observed that herbivory reduced the abundance of RuBPCase activase (RCA) in *N. attenuata.* RCA modulates the activity of RuBPCase (Portis, 1995), a key regulatory enzyme of photosynthetic carbon assimilation, by facilitating the removal of sugar phosphates (ribulose bisphosphate) that prevent substrate binding and carbamylation of the protein's active site.

The regulation of RCA content may optimize plant performance during attack. Reducing RCA protein and transcript levels by gene silencing, similar to elicited plants, decreases both net photosynthetic rates and nitrate assimilation in *N. attenuata*; these reductions in photosynthesis and nitrogen assimilation, in turn, reduced the rate of biomass accumulation (Giri *et al.*, 2006). Since nitrogen and carbon metabolism are linked, crosstalk between signalling pathways that regulate nitrogen assimilation and carbon metabolism is expected (Schachtman and Shin, 2007). Either genetic or environmental manipulations that decrease photosynthesis also inhibit nitrate assimilation (Matt *et al.*, 2002). These studies suggest that herbivore-induced reductions in RCA protein explain, at least in part, the decrease in photosynthetic rates in attacked leaves.

Partial defoliation of individual leaves by herbivores largely increases evapotranspiration via enhanced water loss from cut edges and produces leaf dehydration (Aldea *et al.*, 2005), which not only reduces photosynthesis by causing stomata to close, but also by initiating senescence signalling (Lim *et al.*, 2007). A number of genes are induced by endogenous abscisic acid (ABA) in response to dehydration through the synthesis of the regulating transcription factors MYC and MYB (Yamaguchi-Shinozaki and Shinozaki, 2006). Both MYC and MYB function as *cis*-acting elements which regulate transcription of dehydration-related genes (Abe *et al.*, 1997). Transgenic plants overproducing MYC and MYB had higher osmotic stress tolerance, and microarray analysis indicated the presence of ABA- and jasmonic acid (JA)-inducible genes (Abe *et al.*, 2003). In addition, AtMYC2 is a transcription factor that in arabidopsis functions in JA and JA–ethylene-regulated defence responses (Anderson *et al.*, 2004; Boter *et al.*, 2004; Lorenzo *et al.*, 2004). It has been suggested that crosstalk occurs on AtMYC2 between ABA- and JA-responsive gene expression at the MYC recognition sites in the promoters, and that AtMYC2 is a common transcription factor of ABA and JA pathways in arabidopsis (Yamaguchi-Shinozaki and Shinozaki, 2006).

The lipoxygenase pathway is differentially induced depending on the attacking agent (Heidel and Baldwin, 2004; De Vos *et al.*, 2005; Kempema *et al.*, 2007), and the initiation of jasmonate signalling reduces photosynthesis and vegetative growth. Plants treated with methyl jasmonate develop shorter petioles than control plants (Cipollini, 2005), and arabidopsis mutants that accumulate higher JA concentrations have shorter petioles than wild-type (Bonaventure *et al.*, 2007); these effects of JA on plant growth are modulated by the gene *JASMONATE-ASSOCIATED1* (*JAS1*)

(Yan *et al.*, 2007). Moreover, herbivore-induced JA signalling suppresses regrowth and contributes to apical dominance (Zavala and Baldwin, 2006). It has been suggested that the slower growth and down-regulation of photosynthetic-related genes by herbivore elicitation may be required to free-up resources for defence-related processes (Baldwin, 2001). Herbivore attack produced rapid changes in sink–source relations and increased the allocation of sugars to roots in *N. attenuata* plants; this process is regulated by the β-subunit of SnRK1 (SNF1-related kinase) protein kinase, but is independent of jasmonate signalling (Schwachtje *et al.*, 2006). It is not clear whether the change in carbon allocation affects photosynthetic rate, *per se*, but growth reduction would affect leaf expansion and total plant photosynthesis.

IMAGING METHODS APPLIED TO DAMAGED LEAVES

Chlorophyll fluorescence provides a non-invasive probe which quantifies the component processes related to photosynthetic electron transport and correlates with photosynthetic capacity measured by gas exchange. There are several comprehensive discussions of the theory behind calculating fluorescence parameters and how imaging has been applied to leaf-level physiology (Lenk *et al.*, 2007), aided in crop production practices (Baker and Rosenqvist, 2004), or has been used to screen for stressors and circadian rhythms (Chaerle *et al.*, 2007). High-resolution spatial maps of primary photosynthetic processes, including estimates of the rate of electron transport through PSII, energization of the thylakoid membrane and the quantum efficiency of PSII, not only provide direct estimates of the magnitude of damage but also provide insight into underlying mechanisms (Baker *et al.*, 2001; Oxborough, 2004, 2005).

The mechanisms governing the spatial patterns of photosynthesis following herbivory can be explored further by examining the spatial correspondence of other processes. The ability to collect spatially resolved data for a wide range of molecular, physiological and biophysical processes is increasing dramatically (Chaerle and Van Der Straeten, 2000; Table 1). The damage to water-conducting xylem by chewing insects may generate localized water limitations (Tang *et al.*, 2006). Insofar as these water limitations or other localized changes in leaf chemistry affect stomatal conductance, thermal imaging offers a powerful tool for mapping changes in temperature associated with variation in latent heat flux across leaf surfaces (Jones, 1999; Omasa and Takayama, 2003). With proper calibration, thermal maps can be converted directly into maps of stomata conductance (Jones, 2004; Bajons *et al.*, 2005; Grant *et al.*, 2006). However, because of intrinsic properties of thermal cameras as well as lateral heat transfer within leaves (Jones, 2004), the resolution of thermal images typically is lower than fluorescence images.

The spatial pattern of other components of the photosynthetic machinery, including chlorophyll content and engagement of the xanthophyll cycle (Lichtenthaler *et al.*, 1996; Gamon *et al.*, 1997; Gitelson *et al.*, 2005) are readily mapped with hyperspectral imaging (Chaerle and

TABLE 1. *Representative physiological and molecular processes readily visualized* in vivo *using various imaging methods*

Parameter	Process	Wavelength	Reference
Photosynthesis	F_v/F_m	Maximum quantum efficiency of PSII	470/700	Genty *et al.*, 1989; Rolfe and Scholes, 1995; Oxborough, 2004
	NPQ	Non-photochemical energy dissipation		
	Φ_{PSII}	Quantum yield of electron transport		
Water and energy status	Thermal	Transpiration, conductance	None/ >1200	Jones, 1999; Omasa and Takayama, 2003
	MRI	Water transport	X-rays and microwaves	Gussoni *et al.*, 2001, Clearwater and Clark, 2003
	Tracers		Depends on tracer	Gaff and O-Ogoloa, 1971; Canny, 1990
Leaf pigments	NDVI	Chlorophyll content	$<700/750, 704$	Gamon and Surfus, 1999
	Red/green	Anthocyanin content	$<700/600–699, 500–599$	
	PRI	Xanthophyll cycle	$<700/531, 570$	
Molecular interactions and cell environment	GFP	Gene expression, protein motility, organelle location, cellular pH	485/509	Buschmann *et al.*, 2000; Dixit *et al.*, 2006
	RFP		490, 520, 563/583	
	BFP		UV/440	
Defence compounds	Dyes	Reactive oxygen species, Ca^{2+}	400–700	Fryer *et al.*, 2002; Maffei *et al.*, 2004
Metabolites	Beta emission	Carbohydrate/metabolite transport	Autoradiography	Minchin and Thorpe 2003; Thorpe *et al.*, 2007

Where appropriate, the excitation and measurements wavelengths are noted (wavelength: excitation/measurement).
Modified from Aldea *et al.* (2006*a*).

Van Der Straeten, 2000; Schuerger *et al.*, 2003), though this has not yet been applied to variation within single leaves.

The construction of transgenic plants with the promoter region of a gene of interest connected to a 'reporter gene' permits monitoring of the spatial distribution of transcription, and markers for various organelles, subcellular structures, protein motility and the cellular environment (e.g. pH; Dixit *et al.*, 2006). Genes for firefly luciferase or β-glucuronidase (de Ruijter *et al.*, 2003) have been useful in this regard (Jefferson *et al.*, 1987; Greer *et al.*, 2002); intrinsically fluorescent proteins, such as green, blue and yellow fluorescent proteins, may be more useful partners for *in vivo* imaging studies because of their high quantum yield (Dixit *et al.*, 2006).

In addition to the use of various tracers and dyes for mapping the movement of water, labeling defence compounds (reactive oxygen species) and following transmembrane signals (Ca^{2+}), measurement of beta emissions from carbon isotopes by autoradiography provides a powerful technique for tracking the movement of carbohydrates and metabolites (Kawachi *et al.*, 2006; Thorpe *et al.*, 2007). Beta emissions from ^{11}C are more useful for *in vivo* experiments than ^{14}C, as the particles emitted from the former are short lived and more powerful, thus reducing the logistical problems of handling radioactive waste and providing the capability of penetrating thick plant tissues (Minchin and Thorpe, 2003).

A wealth of information about how herbivory affects photosynthesis and other aspects of leaf physiology could be obtained by applying complementary imaging methods (Table 1) and, if they are applied to the same leaf in one experiment, could provide deeper insight into the mechanisms by which herbivory reduces photosynthesis in the remaining leaf tissue. Combining different images with different resolution is, however, challenging. One approach is to construct simple regressions between the values in aggregate pixels in one image with aggregate pixels in another image. West *et al.* (2005) applied this approach to an examination of the effect of stomatal patchiness (thermal image) on photosynthesis (fluorescence image). Deeper insight can be gained by applying methods of geographical image analysis to physiological data (Omasa and Takayama, 2003; Leinonen and Jones 2004; Aldea *et al.*, 2006*a*). By registering and re-sampling images taken with different instruments, multiple images can be aligned precisely and expressed at a common resolution. Once aligned, new maps are generated that represent the composite information derived from the original separate images (Aldea *et al.*, 2006*a*). The 'image map' of *A. thaliana* damaged by *T. ni* larvae (Fig. 2) revealed that immediately near holes, Φ_{PSII} was greatly reduced and the gene coding for cinnamate-4-hydroxylase (C4H) was strongly induced (red areas). C4H is the first cytochrome P450 monooxygenase in the phenylpropanoid pathway and its induction near damaged areas suggests that a reorientation of metabolism toward defence may have contributed to the loss of photosynthetic efficiency near the cut edges. At greater distances from the edge, other factors contribute to the reduction in quantum efficiency as values of dark-adapted F_v/F_m and C4H expression are low.

LIMITATIONS TO MEASURING GAS EXCHANGE SIMULTANEOUSLY WITH IMAGING

One of the major limitations to estimating herbivore-induced effects on photosynthesis is correctly characterizing CO_2 diffusion and uptake within the leaf. Gas exchange measurements typically are used to generate a relationship between photosynthetic assimilation and internal [CO_2] – the A/C_i response curve. This relationship assumes leaves have homogenous distribution of chloroplasts (for light absorption) and of stomata (for gas exchange; von Caemmerer, 2000). Heterogeneity across remaining leaf tissues caused by herbivory may compromise the utility of the A/C_i response curve. In addition, gas exchange chambers enclosing leaves reduce internal CO_2 where gaskets overlay leaf area through shading-induced stomatal closure (Pieruschka *et al.*, 2006). Diffusion of CO_2 may also occur laterally, with respect to morphology, and may diffuse 2 mm in homobaric and up to 1 mm in heterobaric (compartmentalized) leaves (Pieruschka *et al.*, 2006; Morison *et al.*, 2007). Heterogeneity in photosynthesis caused by non-uniform CO_2 uptake, in addition to lateral diffusion of CO_2 within

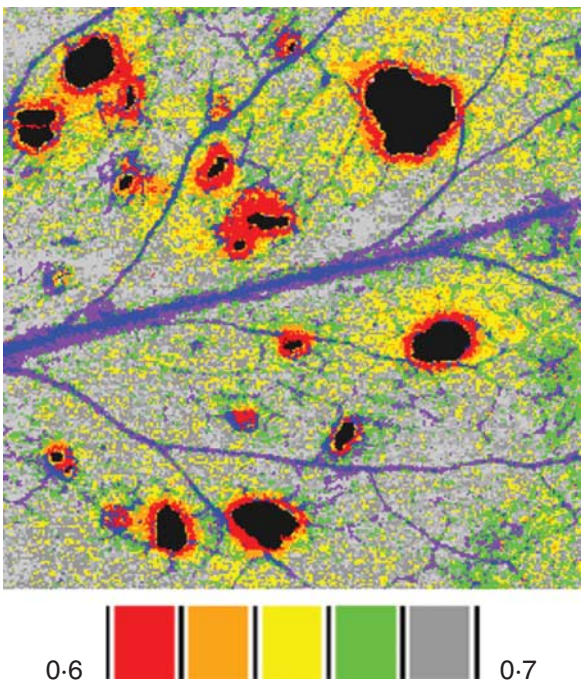

FIG. 2. False colour images of the location of damage classes surrounding holes in an arabidopsis leaf exposed to herbivory by *Trichoplusia ni* larvae. Transgenic *Arabidopsis thaliana* carried a cinnamate-4-hydroxylase (C4H) promoter and β-glucuronidase (GUS) reporter gene fusion. In *A. thaliana*, enzymes in the phenylpropanoid pathway may contribute to defence against pathogens; C4H is constitutively expressed in the veins of undamaged leaves and induced by wounding near the site of damage. The image was constructed by combining independent images of the same leaf of chlorophyll fluorescence (Φ_{PSII}) and GUS staining for C4H activity using geographic image analysis software. The false-colour scale bars indicate the mean value of Φ_{PSII} for each damage class. The veins shown in blue and purple were classes that were excluded from analysis because their high level of GUS staining was not related to herbivory. Data were generously provided by Dr Jennie Tang.

leaves, will interact with heterogeneity induced by feeding damage when scales are similar. For example, defoliation damage may reduce Φ_{PSII} within a distance of 1–2 mm (Aldea *et al.*, 2005, 2006*b*); however, CO_2 diffusion through cut edges into damaged tissues and adjacent undamaged tissues, may increase C_i and alleviate the suppression or even enhance photosynthesis.

CONCLUSIONS

In many cases, arthropod damage reduces photosynthesis to a greater extent than would be predicted by the direct loss of leaf tissue. With the use of new imaging technologies we are beginning to understand how photosynthesis and water balance are modulated in undamaged tissue following herbivory. Connecting these alterations in physiology to changes in gene transcription and hormonal signalling will increase our ability to estimate whole-plant responses to herbivory, and will improve our estimates of the impact of herbivory on higher levels of biological organization, such as yield loss and assessments of overall ecosystem productivity.

Indirect alterations of photosynthesis have been identified across multiple plant systems and can be categorized by plant responses. Severed vasculature increases transpiration, reduces Φ_{PSII}, and reduces NPQ, whereas sink demands of galls enhance transpiration. Photosynthesis is greatly reduced through the release of toxic secondary compounds or defences elicited by herbivore attack. Even the initiation of these defences triggers down-regulation of photosynthetic component processes or proteins. Despite these characterized indirect effects, investigations are lacking for some damage types (e.g. specialized cell content feeders) and their subsequent interactions with primary and secondary metabolite pools.

While we are closer to elucidating the mechanisms responsible for herbivore-induced alterations in photosynthesis and related processes in undamaged tissues, a complete understanding of how the indirect suppression of photosynthesis propagates away from the point of damage remains unknown. Genomic analyses of plants challenged by arthropods have revealed a trend for down-regulation of photosynthesis-related genes, but a closer look at transcriptional changes between and within feeding guilds has identified differential regulation of defence genes and overlap among damage guilds. A universal response to herbivory is the induction of the lipoxygenase pathway, but attacking agents differentially induce this pathway and corresponding jasmonate concentrations (Heidel and Baldwin, 2004; De Vos *et al.*, 2005; Kempema *et al.*, 2007). Differences in concentrations of defence signalling molecules may lead to differential down-regulation of photosynthesis genes. Already, the overlap in the magnitude of down-regulation has been noted between caterpillars and general cell content feeders compared with aphids (Voelckel *et al.*, 2004), leading to species-specific regulation of different metabolic pathways (e.g. nitrogen metabolism by aphids). Subsequently, within-plant mechanisms underlying the indirect effect, and not the direct effect, may drive physiological responses in future plant–insect interactions.

ACKNOWLEDGEMENTS

We thank S. Davis, K. Teixeira and S. H. Woodard for constructive comments on an earlier version of this manuscript. We thank Dr Arthur Zangerl for the concept behind Fig. 1 and Dr Jennie Tang for conducting the experiment that produced Fig. 2. We acknowledge generous support from the Office of Science (BER), US Department of Energy, grant no. DE-FG02-04ER63489, and the National Science Foundation, grant no. IBN 0326053.

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